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Impact of Climate Change on Northern Vegetation Limits and Forest Tree Wind Seed Dynamics from the *Last Glacial Maximum* to Present

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§ In Memory of Irena Naydenova

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Abstract

Seeds interact with climate and soil factors during their dispersal, determining the natural distribution areas of species and influencing their geographic fluctuations. These fundamental roles have a significant impact on species evolution and population genetic robustness at the perpetual abiotic change of

the ecological conditions. The study investigates the distribution of ice during the *Last Glacial Maximum* (*LGM*) and its effect on the tree line in forested areas.

We compared the hypothesis of the *LGM*'s permanent ice extent and its impact on vegetation limits with the speed of forest tree seed dispersal. Our analysis suggests that the permanent ice cover during the *LGM* was likely more restricted and fragmented than initially believed. The presence of multiple micro refugia along the current tree line was located no more than 150 km from the present-day northern tree distribution. This observation does not contradict the extent of the ice sheet in the Northern Hemisphere during the *Last Glacial Maximum* (*LGM*).

1. Seed radiation and vegetation

Seed dispersal is a critical process for maintaining the natural distribution area of spermatophyte plants, as well as for their migration and role in ecosystem succession (Stefanov 1943, Prestianni 2010). The movement of seeds from the parent trees to the new free areas, where the next generation will be established, is essential for species survival in the landscape. Seeds also serve as a food source for many animals, with some species relying on them as a primary survival resource. Each seed has species-specific morphological, physiological, and nutritive characteristics that influence its dispersal, collectively referred to as dispersal syndromes. These traits include seed size, forms, colors, mass, persistence, nutrition tissues (metabolic syndrome), protection mechanism from predation, level of annual seed production, the start time of ripening, and seed radiations model (or models). Additional factors include the parent's physical structure (form and size), and forest composition as a group of individuals of the same species, which can influence the spatial structure of seed dispersal (Seed: morphology general – Howe & Smallwood 1982; Bullock et al., 2006; Green et al., 2022). Each characteristic mentioned here is subject to selection pressure (direct and/ or indirect); often driven by animal behavior. The evolution of seed dispersal syndrome reflects a balance between successful seed radiation vs. combatting other selective pressures. Vegetation migration is dynamic over time, influenced by complex interactions between biotic and abiotic factors, which is important for phylogeographic analysis and assessing the impact of climate change on vegetation.

For a long time, the natural seed dispersal distance for forest trees has been a key question in forest management and reforestation practices. Over the past 300 years, many European countries developed different sylviculturural practices with relatively different intensity timber harvesting as shelterwood cutting; seed-tree method; uneven-aged forestry; group selection cutting; strip-and-group felling system; shelterwood wedge cutting; mixed-form regeneration methods; continuous cover forestry; uneven-aged forestry; selection forest; and target diameter harvesting according to Hawley & Smith (1954), Nyland (2002). These methods are still used in Continental and Temperate climatic group regions. Of the different sylvicultural practices cited above, the natural reforestation success for coniferous trees was calculated at a seed dispersal distance of less than 50 meters per generation. One generation includes the time required for trees to reach stable reproductive capacity, meaning consistent production of viable female flowers and pollen. For

example, based on limited studies of seed production in the pines, the survival ratio from dispersed seeds to trees reaching reproductive age is often less than 10^{-5} for the forest tree (Calama et al., 2017).

The seed dispersal success depends on the morphological, and biological characteristics of the seeds, as well as environmental conditions such as temperature, moisture, soil conditions, and predations. The vector of seed dispersal is diverse with the most common being wind (*anemochory*), water (*hydrochory*), gravity (*barochory*), animals (*zoochory*), including mammals (*mammalochory*), birds (*ornithochory*), reptiles, fish, and insects. Animal-mediated dispersal may involve ingestion and defecation of seeds (*endozoochory*), transport via mouthparts (*synzoochory*), or accidental transport (*epizoochory*). For the all combination analyzed, the species vs. vector of seed dispersions persist "secondary dispersal", "indirect dispersal" or «two-phase dispersal», known as a *diplochory* (Vander et al. 2004). The secondary dispersal is a result of more than one radiation vector. Generally, secondary seed radiation makes a relatively low contribution to the total seed migration distance with a very short distance and a high loss to seed by animal predation (Wall et al., 2004). D*iplochory* is ignored in the proposed model here due to its very low contribution of seed radiation. Among the dispersal vectors, wind dispersal appears most significant in continental, temperate, and polar regions, where climatic fluctuations are a major abiotic factor. The climatic regions referred to in this study follow the Köppen climate classification (1918). This phenomenon of the migration rate and climatic changes interrelation will be explored in more detail in the next sections.

2. Wind seed radiation and the factor, limit and empirical data

Seed radiation by wind is one of the principal methods for migration. The seeds of these plants have developed a lot of different morphological «wing structures» known as *anemochory* flyers through long evolution processes and high selective pressure. These structures include rollers, throwers, dust diaspores, balloons, plumed and or wings (Howe & Smallwood 1982; Bullock et al., 2006; Green et al., 2022). These adaptations aim to increase maximum seed dispersion distance in canopy trees or open habitats, increasing the chances of successful germination. In the context of natural plant colonization, also known as the vegetation dispersal syndrome, it is important to distinguish between "*simple or physical seed dispersal radius*" and "*effective seed dispersal radius*". The latter refers to the successful establishment of new plants, which includes seed germination followed by the establishment of sustainable populations. Sustainable populations are defined as multiple generations present in a specific location, which implies successful seed production and survival from seedlings to reproductive individuals. The *effective seed dispersal radius* depends on seed density and ecological conditions and includes stages such as primary dispersal, post-dispersal seed predation, germination, seedling emergence, and survival to reproductive age. The long-term migration patterns of

vegetation depend on numerous abiotic factors, including natural disturbances like forest fires and climatic fluctuations.

The factors determining long-distance seed dispersal include the plant habitus (growth form) of the mother plant, seed wing structure, and ecological conditions. Seed dispersal within the crown of a tree is considered the "minimal distance" and insignificant for plant migration and colonization of new areas. Over the last 35 years, numerous empirical mathematical models have been developed to simulate wind dispersal incorporating factors such as wind speed, wind frequency, wind direction, spatial structure (i.e., forest type, forest density, or open landscape), and height of the canopy and mother plants (Nathan et al. 2002a, b, 2011). Field experiments have shown that the average dispersal distance is species-dependent, often within less than 50 meters (Levin and Kerster, 1974; Gonzalez-Martınez et al. 2002; Robledo-Arnuncio & Gil, 2005). The empirical analysis indicates that seed dispersal distance is better correlated with plant height than seed mass (Thompson & Rabinowitz, 1989; Moles & Leishman 2008; Thomson et al. 2011). Logically the tail species tend to have long periods to reach reproductive age as forest trees versus herbaceous species. This period for forest trees is generally between 10 and 20 years (Wright 1976, Dobrinov et al. 1982; Alexandrov et al. 1988; Vidacovic 1991; Greene & Johnson 1993; Calama et al. 2017). In contrast, shorter species such as those in the *Poaceae* family can reach reproductive capacity in their first growing season. This distinction is crucial for understanding species life-history strategies, forest community succession, and evolutionary patterns. For additional information on the maximum seed dispersal distance for forest trees, refer to Figs. 1a, b (Seed dispersal distance by species and authors). It is important to note that the mean random dispersion distance is often close to or greater than the effective seed dispersal radius, and the maximum recorded seed dispersal distance is about 2-3 times longer than the mean dispersal distance.

In the next paragraph, we will conduct a simple calculation comparing the theoretical migration speed of the herbaceous model species (*G-SM*) and a forest tree model species (*T-SM*). These model species projected migration distances and migration rates represent «*sens lato*» typical characteristics of their respective groups. Let's explore this in more detail in the following section.

Simple modeling of seed wind radiations difference between forest tree vs herbaceous plant

One important question is why we chose model species instead of specific ones. The simple answer is twofold: first, we aim to calculate the maximum possible migration distance under the hypothesis of perfect ecological factors over a long historical period. Second, by avoiding the inclusion of specific physiological or morphological traits for each specificity group (and for each species within each group), we prevent unnecessary complexity that could divert the focus from the main objective of understanding maximum plant migration distances and their relationship to climate
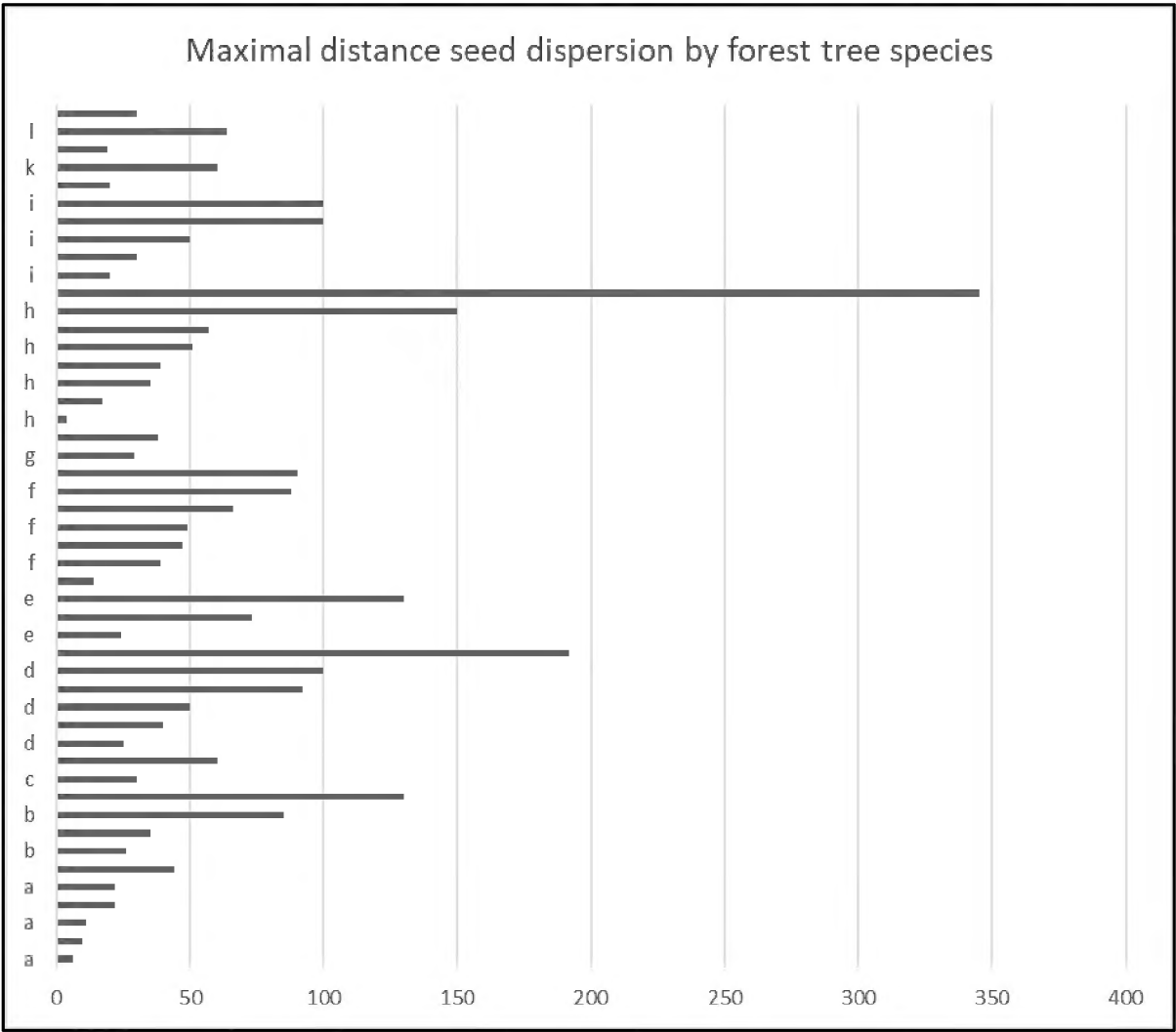
Fig. 1a. The maximum forest tree seed radiation distance: [a]*Abies* (Kutter & Gratzer 2006; Paluch, 2011; De Andres et al. 2014; Paluch et al. 2019), [b]*Acer (*Diaci & Thormann, 2002; Schutt et al. 2003; Hein et al. 2009; Diaci et al. 2011*),* [c]*Alnus* (McVean, 1956; Kellomäki et al. 1987), [d]*Betula* (Sarvas, 1948, 1952; Karlsson & Albrektson, 2001; Hynynen et al. 2009; Hunt et al. 2013), [e]*Carpinus* (Kohlermann, 1950; Bouman et al. 2000), [f]*Fraxinus* (Stoyan & Wagner, 2001; Heuertz et al. 2003; Wagner et al. 2004; Schmiedel et al. 2013), [g]*Larix* (Kohlermann, 1950; Kellomäki et al. 1987), [h]*Picea* (Kohlermann, 1950; Diaci et al. 2005; Kutter & Gratzer, 2006; Dovciak et al. 2008; Piotti et al. 2009), [i]*Pinus* (Kellomaki et al. 1987; Dovciak et al. 2005; Mukassabi et al. 2012; Przybylski et al. 2021; Simental-Rodriguez et al. 2021), [k]*Pseudotsuga* (Isaac, 1930; Tschopp et al. 2015), [l]*Tilia* (Kohlermann, 1950), and [m]*Ulmus* (Venturas et al. 2014a, 2015). The distance is presented at horizontal grid of 50 m.

change. Additionally, anyone interested in conducting specific analyses of projected migration distances and migration rates will find it easy to adapt their data to this simple model.

The aforementioned characteristics of seed dispersal raise the question: What is the difference in migration speed between forest trees and herbaceous (i.e. grass) species, and how does this affect phylogeography? To address this, we created a simple model using the same 50m seed dispersal distance but with different reproductive ages – one year for the herbaceous model species (*G-SM*); and 10 years for forest tree model species (*T-SM*). This predicts that grass species would migrate 10 times faster than forest trees.
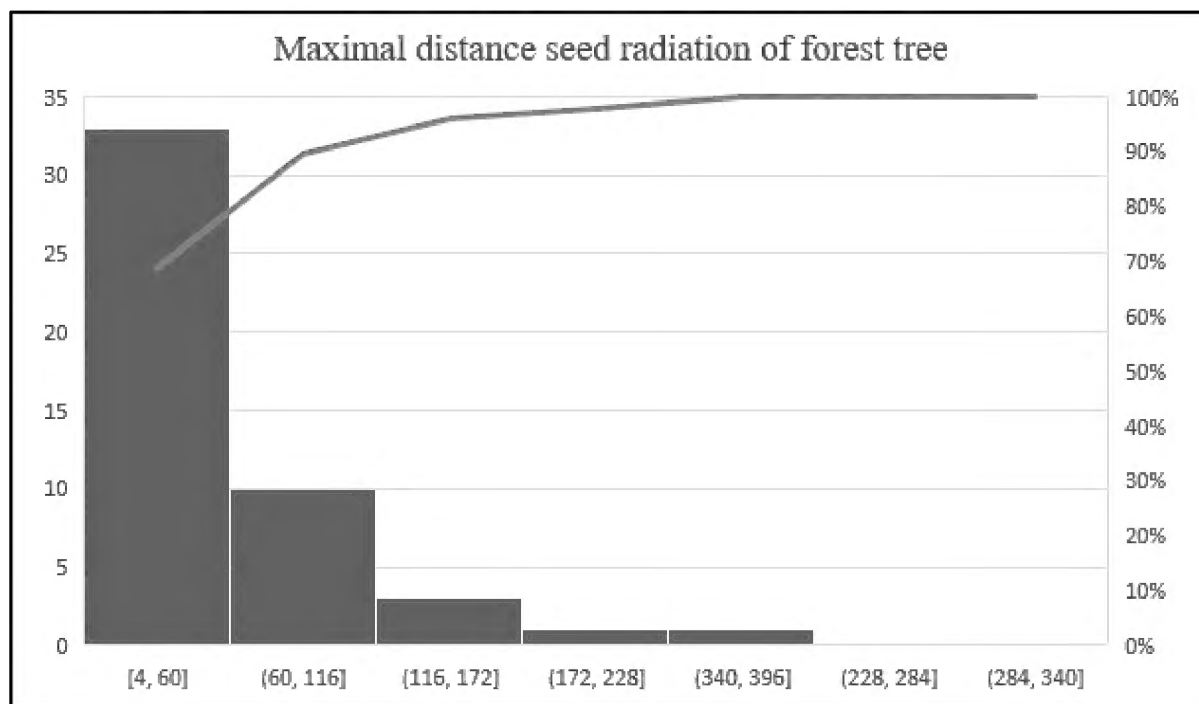
Fig. 1b. The summary statistic of the average maximum distance for forest trees from boreal and temperate regions by 5 classes of radius of physical seed distribution. The red line presents the accumulative % of used bibliography.

The migration speed of grass plants proposed here is well correlated with the spread of invasive herbaceous plants in North America after colonization by farmers in the 18th century, according to the North American Invasive Species Network (www.naisn.org). The same organization presents a list of 375 tree and herbaceous species brought to North America by farmers, along with secondary radiations. For example, one of the radiation champions, dandelion (*Taraxacum officinale*), shows a migration distance of up to 100 meters per year for viable seeds, according to Tackenberg et al. (2003). Generally, the radiation distance per year (rates) for all invasive herbaceous plants from North America falls within the proposed limits of our projected model. The migration distance per year for invasive trees from North America is similar to that shown in Fig 1a.

We assume there is great variability between species in each group of trees and herbaceous species. Our investigation is focused on testing the general hypothesis of maximum plant post-glacial migration rates, rather than exploring differences between species. We used multiple proven empirical data sets in our simple model, collected from practical observations in agroforestry fields across multiple countries over the last century for a large list of species. In contrast to our methodology, several publications have ignored proven empirical data collected from current agroforestry field observations and have preferred to use paleo-botanical records (Svenning et al. 2007, 2008; Feurdean et al. 2013).

Currently, the northern herbaceous line limit and the forest tree line limit are well-determined (Fig. 2). For more information, see Bennett et al. (1991), Bhagwat and Willis (2008), Stroeven et al. (2016). The difference between these two limits raises the question: Where were the herbaceous vegetation line and forest tree lines

during the period of the Last Glacial Maximum (*LGM*)? Some contemporary publications ignore this difference and consider similar migration speeds for both groups of vegetation. Some of them speculate that forest tree migration distance from the Continental and Temperate climatic group region up to the Tundra/Boreal biome (i.e., Tundra sub-group climate) over a period of less than 27 000 thousand years (Gamache et al. 2003; Jamillo-Correa et al. 2004; Godbout et al. 2005; Naydenov et al. 2007). These speculations involve migration distances spanning thousands of kilometers since the *LGM*, which we discuss here.

From our initial parameter, the herbaceous model species (*G-SM*) could migrate a maximum of 50 km in 1 000 years leading to a potential migration of 1 500 km for over 30 000 years. This period covers the last glacial maximum (*LGM*) considered to be 27 000 years ago. In contrast, the reproductive age of forest trees (*T-SM*) is 10 times longer (10 years), meaning their maximum migration distance would be only 150 km over 30 000 years. If we consider that the post-glacial migration is after LGM – i.e. 20 000 years ago, the calculated distances are 1000 km for herbaceous and 100 km for trees respectively. This brings us to the "*Northern Vegetation Limit Line Dynamic Dilemma*." Based on the calculated maximum migration distances, we can conclude that during the *LGM*, there was the presence of
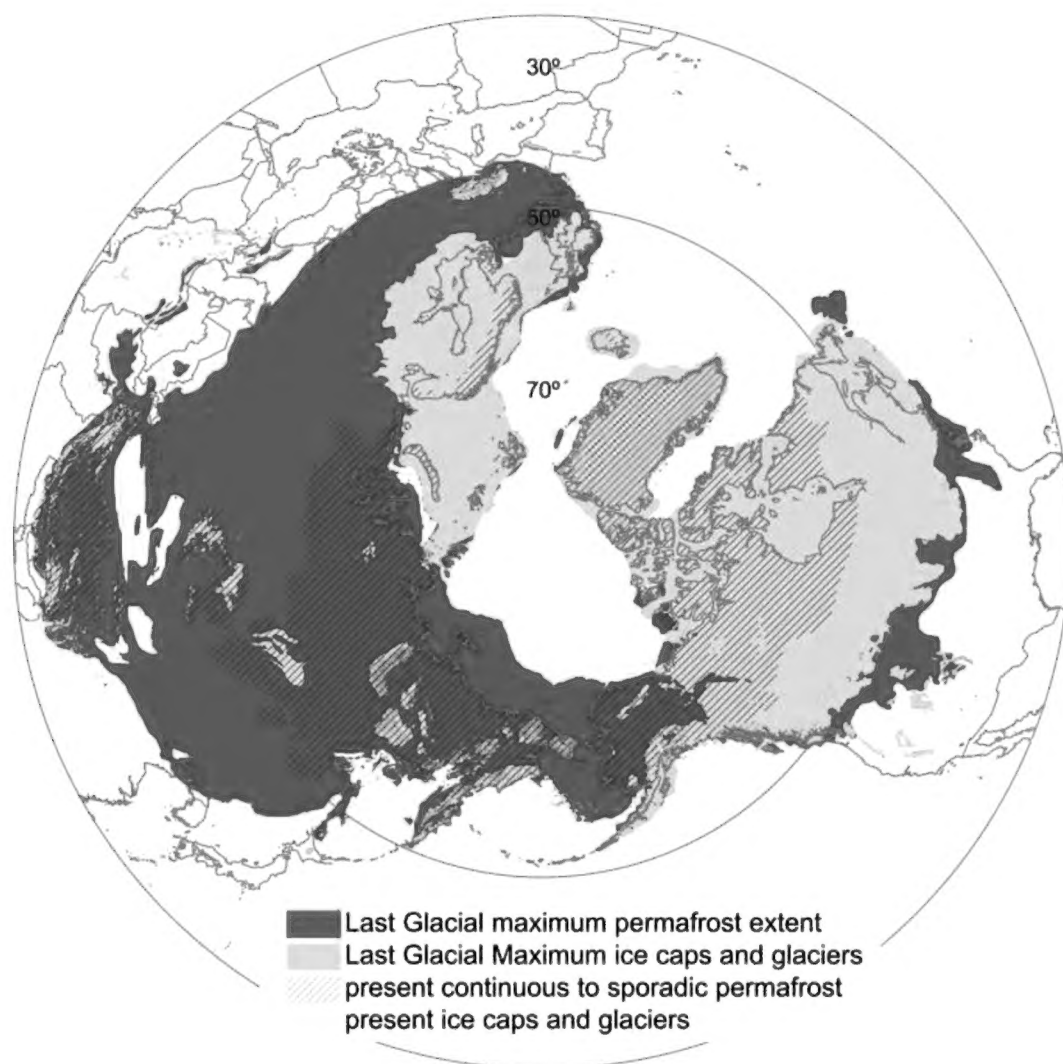

Fig. 2. The comparative area of distribution of the ICE shell and permafrost limit at present day vs. from Last Glacial Maximum (*LGM*) according to van Huissteden (2020).

multiple micro refugia no more than 150 km from the current position of the forest tree line. This statement is not in contradiction with the ice sheet limit in the Northern Hemisphere during the *LGM* (see Fig. 2). This contradicts descriptions of the LGM ice sheet limit and the frequently hypothesized post-glacial migration patterns based on paleo-botanical records, which suggest much greater migration distances than our model calculates (Svenning et al., 2007, 2008). For example, Feurdean et al. (2013: Table 1) suggest migration distances for *Abies alba* of 1 100 km, *Picea* of 500 km, and *Pinus* of 1 550 km, with migration speeds of 60-260 m per year. In our methodology, we preferred to use proven empirical data collected from practical observations in agro-forestry fields today, rather than relying on paleo-botanical records. The reason for this choice is the well-known, long standing issue of the low credibility of paleo-botanical records due to possible bias in fossil preservation, incomplete sampling, and taphonomic processes. For example, the number of species known through the fossil record is less than 5% of the number of species alive today. In the next paragraph, we will explore this discrepancy in more detail.

Impact of *LGM* and climate change on plant area of distribution

The continental and macro – geographic ice shell structure, and place dilemma during, the *LGM* have been a subject of debate. A coherent perspective on this issue must arise from a logical combination of proven data from the practices observations from the agro-forestry field at present days and analysis. The initial idea was based on some simple climatic data interpolations under different temperature change scenarios, which depicted a continuous ice sheet covering a large area of the Northern Hemisphere. However, if this were true, as we have demonstrated, the majority of Tundra/ Boreal Forest tree species would not have been able to reach their present-day tree line (see Fig. 3). "Taiga" is commonly used to describe this biome in the Eurasia region, while "Boreal" refers to the same biome but in North America. Let us consider this using our simple model.

The Tundra/Boreal biome is characterized by coniferous forests, predominantly consisting mostly of pines, spruces, and larches. According to our example for 27 000 years post *LGM* period, the maximum distance for these forest trees could only have been around 135 km in the extreme northern part of its ancient distribution, assuming no natural disasters took place such as forest fires, climatic inversion, diseases, or predation by insects and animals. In the southern part, where forest trees from mixed-composition forests in the Continental and Temperate climate zones face high competition, the migration distance over the same period could be less than 67–68 km (approximately 50% of the northern distance). In comparison, herbaceous in southern areas could have migrated between 675 and 1 350 km toward the northern limit. According to our hypothesis, there is a significant difference between the migration speed of forest trees and herbaceous species. Many examples support this hypothesis.
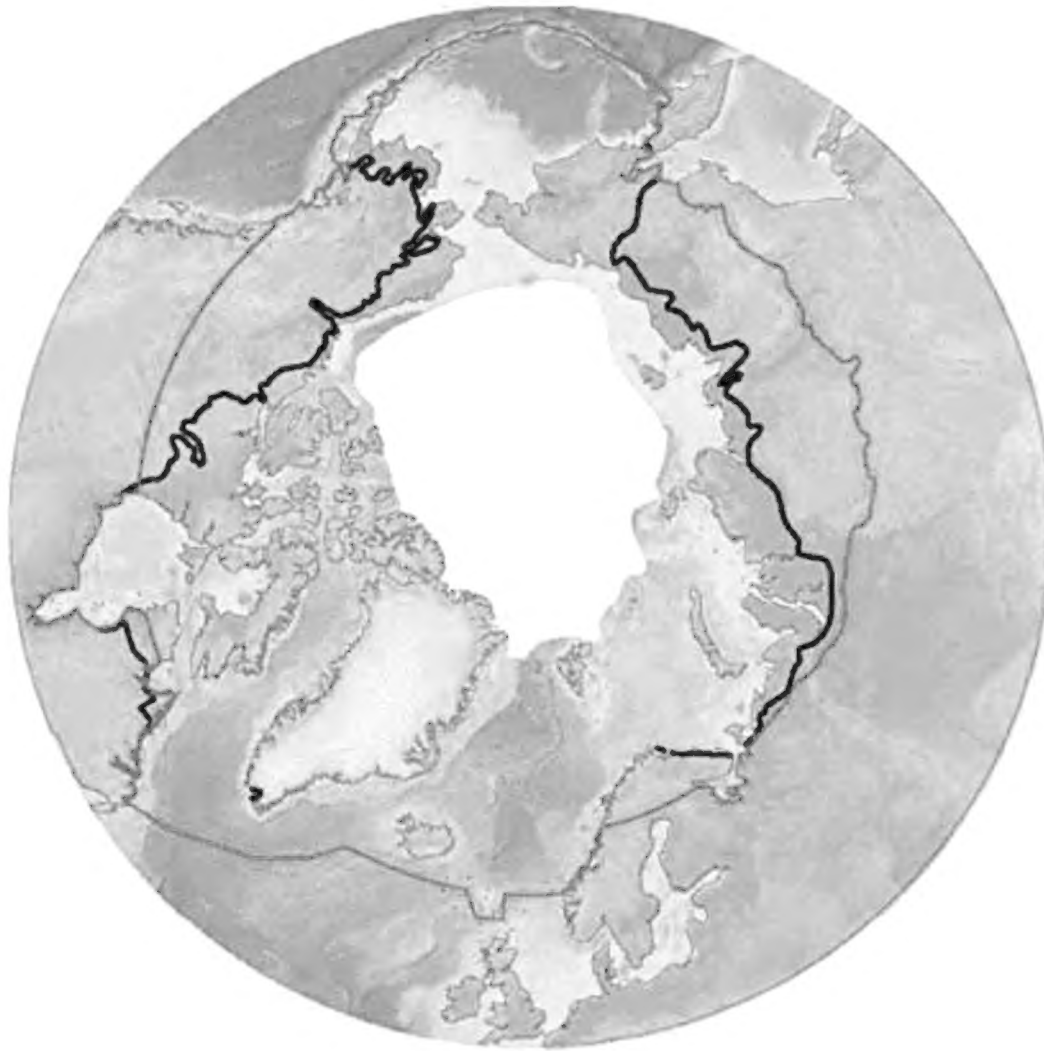
Fig. 3. The present northern tree line in the Arctic according to UNEP/GRID. Boreal forest occurs only to the south of the tree line (the dark green line on the graphic). The Arctic area, as defined by the Arctic Monitoring and Assessment Program (AMAP), is limited by the orange line on the graphic.

    Note-1: According to our modeling, the historical northern tree line in the Arctic from the Last Glacial Maximum (*LGM*) period must be at 150 km in the southern direction. Image Credit: Hugo Ahlenius, UNEP/GRID-Arendal

For instance, the Beringia land bridge is well-documented during the *LGM*, connecting Asia and North America with a contact zone as wide as 2,000 km (Fig. 4). The bridge between Alaska and Kamchatka (i.e., between western and eastern Beringia) was no more than 250- 350 km wide. Despite this, no forest tree species from the Tundra/Boreal biome – such as those from the genera *Pinus, Abies, Picea, Thuja, Juniperus, Larix, Populus,* or *Betula* – with wind-dispersed seeds crossed this bridge. In contrast, species like Homo sapiens, animals (e.g., *Canis lupus*), and plants with zoochorous seed dispersal mechanisms (e.g., *Vaccinium uliginosum and Saxifraga oppositifolia*) did successfully cross the bridge (DeChaine 2008; Koblmuller et al. 2016). Additionally, the existence of large grasslands in the Tundra/Boreal biomes artifact of woolly mammoth (*Mammuthus primigenius*) and woolly rhinoceros (*Coelodonta antiquitatis*) from *LGM* confirm significant grassland persistence. Another supporting argument comes from forest management in Europe
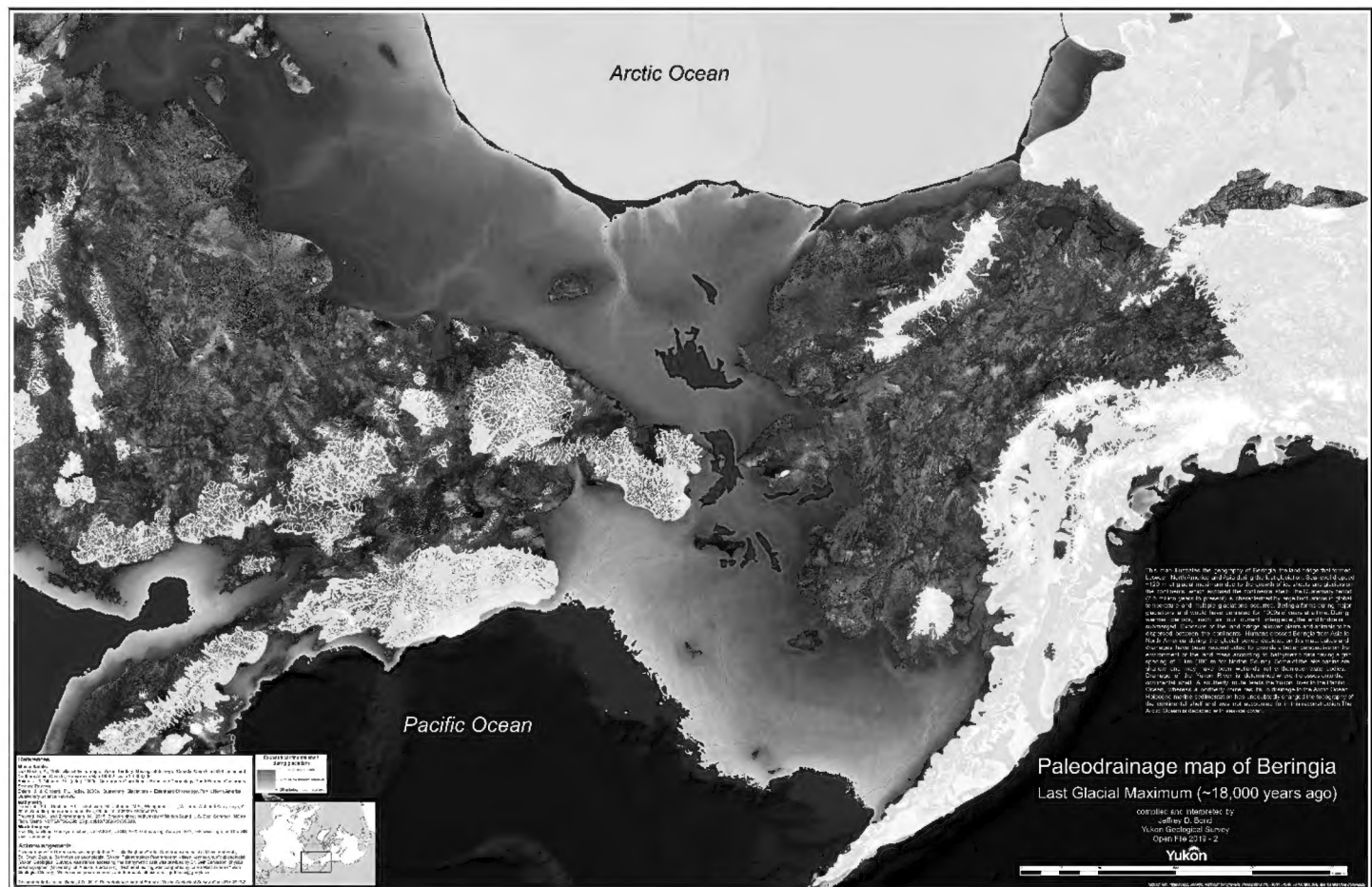
Fig. 4. The simulative paleo map of Beringia passage from Last Glacial Maximum.

and North America over the last half-century, which show similar natural forest tree migration rates to those proposed by our hypothesis (Hawley & Smith, 1954; Nyland, 2002).

Natural disturbances such as forest fires, insect infestations, and flooding are common in the Tundra/Boreal biome region (i.e., Tundra sub – group climate) now and were likely just as frequent during the post-*LGM* period. We hypothesize that a continuous, monotone ice sheet likely never existed. Instead, it was fragmented by climatic interactions around watersheds, where most forest tree species could have survived. The multiple micro refugia were probably no more than 150 km south of its current position. The climate was cool with the very short summer in the ice shell southern limit. As one moved further north, summers became increasingly shorter in both duration and intensity, likely to the point where in some extreme northern regions, there were no true summers – just extended spring and fall seasons with varying intensity. This would explain the presence of permafrost and paleobotanical records in these regions. The composition of plant ecosystems was very different for herbaceous species compared to forest trees. That hypothesis helps resolve the vegetation limit line dynamic dilemma and sheds light on the limited effectiveness of forest tree wind-dispersed seeds following the *LGM*.

The long forest tree migration distance for the post glacial depression period must be revised. We believe that the *long migration distance forest tree species* are resulting from millions of years of constant migration pressing to now involving pre-

sent forest tree species and their ancestors (Naydenov et al. 2014, 2016, 2017). That is particularly important for molecular phylogeography analysis using low mutation rate molecular markers (Naydenov et al., 2024). This migration pressing is constant with low intensity and is a result of natural forest tree species area expansion and humidity attraction interactions. For example, *Pinus nigra* western forward migration tendency from continental and dry climate European region (Naydenov et al. 2024). The same tendencies for Black Pine are observed here from southern to northern Turkey. The *humidity attraction center* was observed for multiple species (Cooper et al. 1995; Demesure et al. 1996; Dumolin-Lapègue et al. 1997; Sperisen et al. 2001; Giesecke & Bennett, 2004).

Northern peripheral forest tree population particularity

The migration step of seed plants into regions with favorable ecological conditions occurs throughout one reproductive generation. However, as discussed earlier, the period for one generation of forest trees compared to herbaceous plants is vastly different. Another factor affecting migration is the frequency of seed production in populations located at the tree line of the species' distribution. Numerous observations have shown that forest trees at the northern limit of their range produce seeds far less frequently than central populations. For some species, seed production cycles are 3 to 5 times longer in peripheral populations (Wright 1976; Grant 1980), which further slows the migration process after the ice sheets begin to melt. Thus, northern forest tree migration following the *LGM* would have been 3 to 5 times slower than expected. Based on the data discussed earlier, the migration speed of northern forest trees – estimated at around 50 meters per generation – could take 60 to 100 years per step. This is a notably slow pace compared to herbaceous plants. However, one advantage forest tree seeds have over herbaceous seeds is their superior ability to survive cold and harsh winter conditions, which helps them persist in northern climates. For this reason, the migration speed proposed in our simple model should be considered a very optimistic estimate. This leads to a strong argument for revising the assumed extent of permanent ice regions during the *LGM* and their impact on historical vegetation fluctuations from a phylogeographic perspective.

Conclusion

The results obtained from the simple model based on the proven data from the practices observations from agro-forestry field at present days and analysis showed presence of the multiple micro refugia participle in the present tree line was no more than 150 km from the present-day northern tree distribution. This statement is not in contradiction with the ice shield limit in the Northern hemisphere during *LGM*.

Our analysis suggests that the permanent ice cover during the *LGM* was likely more restricted and fragmented than initially believed; combined with significantly frequent climatic fluctuation at micro geographic schedule.

In the perspective of climatic change it is important to consider more intensive protection and management of biodiversity by significant amount and territory of natural reserves combined with protection from forest fire and illegal harvesting.

In conclusion, the *long migration distance of forest tree species* is not related to the post – *LGM* species expansion, and it is better to be interpreted as a *very long historical temp migration*. That conclusion holds for the majority of forest tree species.

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Conflict of interest: None declared.

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